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The palaeopsychrosphere in the Devonian

Sylvie Crasquin & David J. Horne

The interpretation of Palaeozoic marine benthonic ostracods of the Thuringian "Ecotype" or "Mega-assemblage" as indicative of a palaeopsychrosphere has been controversial. We review the evidence and conclude that the characteristics and distribution of these ostracods are consistent with the existence of deep, cold, well-oxygenated water masses, formed by high-latitude sinking of surface waters, in the Devonian oceans, comparable with those of the modern ocean that constitute the psychrosphere (waters below the thermocline with temperature <10 °C). We present a new palaeoceanographic model for the Frasnian-Famennian (Late Devonian) Kellwasser events that resulted in the extinction of 75% of marine ostracod taxa, mostly neritic or pelagic forms, while the deep-water Thuringian Mega-assemblage was relatively unaffected. We offer an explanation for the unlikely preservation of examples of such a deep-water (bathyal to abyssal) ostracod fauna that involves upwelling of deep cold waters on continental margins.

Keywords
Devonian, marine ostracods, palaeoceanography, palaeopsychrosphere, Thuringian Mega-assemblage, deep cold water, Frasnian-Famennian Crisis

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In the present-day ocean the psychrosphere (Bruun 1957) consists of watermasses with temperatures <10°C that lie below the thermocline, typically in bathyal and abyssal depths with an upper limit as deep as 700m (shallowing to as little as 100m in upwelling regions) but approaching the surface in high latitudes; in contrast, warm surface waters constitute the thermosphere. The ocean floor bathed by these deep, cold waters is inhabited by a diverse and distinctive benthonic ostracod fauna, fossil assemblages of which have been used to demonstrate that the modern psychrosphere has existed since the Early Cenozoic (Benson & Sylvester-Bradley 1971; Benson 1988). The term "psychrosphere" is now used rarely by anyone but ostracodologists, but it still has some utility when applied to ancient oceans and their fossil ostracod assemblages, the study of which may shed new light on the nature of Palaeozoic – Mesozoic deep ocean circulation. The existence of a palaeopsychrosphere during the Palaeozoic (Kozur 1972, 1991) has been postulated on the evidence of a distinctive ostracod fauna known as the Thuringian Ecotype (Zagora 1968; Bandel & Becker 1975), members of which show morphological similarities (such as thin-shelled and spiny carapaces) with those of the modern psychrospheric fauna. This interpretation has been much debated, however (Lethiers & Crasquin 1987; Becker 2000b), as have the nature of deep ocean circulation through the Phanerozoic (Horne 1999) and its role in marine biological crises such as the Late Devonian Kellwasser and Hangenberg extinction events (Chen *et al.* 2013; Carmichael *et al.* 2014, 2016). Here we review the concept of a palaeopsychrospheric ostracod fauna in the context of global ocean circulation and marine

extinction events in the Devonian period, and propose a new model for the origin, preservation and survival of the Thuringian Ecotype assemblage.

The Thuringian Ecotype and the palaeopsychrosphere

The Thuringian Ecotype is the name given to a special association of Ordovician-Carboniferous benthonic marine ostracods by Becker (*in* Bandel & Becker 1975), characterised by taxa with distinctively prominent spines on their valves (but including taxa without spines) and found in very deep water (bathyal) facies, in contrast to the benthonic "Eifelian Ecotype" association typical of shallow platform settings. According to Kozur (1991), Becker adapted the term from "Thuringian typus" introduced by Zagora (1968). Becker (1982) considered that the Thuringian Ecotype existed from the Ordovician (citing Blumenstengel 1965) to the Triassic (citing Kozur 1970). Members of the podocopid families Tricorninidae, Bythocytheridae, Bairdiidae, Rectonariidae and the platycopid (metacopine) Family Healdiidae, are particularly significant components of the Thuringian Ecotype (Lethiers & Raymond 1991) along with genera from other families (Table 1). Becker (1991) called this association the "Thuringian eco-assemblage".

Kozur (1991) argued that "Thuringian" and "Eifelian", already in use as stratigraphical terms, were misleading for palaeoenvironmental associations, and preferred to call the Palaeozoic Thuringian faunas "palaeopsychrospheric" (Kozur 1972) because of what he regarded as striking similarities (in terms of morphology, distribution and distinction from shallow-water faunas) with Tertiary–Recent psychrospheric faunas and because the intervening Jurassic–Cretaceous oceans apparently lack such faunas and were supposedly thermospheric (i.e. with warm bottom waters). In Kozur's view the palaeopsychrospheric fauna was restricted to environments with minimum depth limits of 200 to 500m and having deep water connections with the world ocean, with occurrences estimated to be as deep as 1,000 to 2,000m, and existed from the Silurian to the Triassic (Kozur 1972, 1991).

Schallreuter & Siveter (1985) observed that the existence of a Lower Palaeozoic psychrospheric ostracod fauna was undocumented, but nevertheless considered that conditions suitable for the formation of cold deep water in the ocean (and thus an equivalent of the modern psychrosphere) were possible during the Ordovician. Futhermore, many forms present in the Ordovician – Silurian have morphologies close to Thuringian Ecotype forms. Schallreuter (1971) illustrated a few spiny taxa from the late Ordovician that are reminiscent of Upper Palaeozoic Thuringian Ecotype assemblage morphologies; most notable among these is *Pseudohippula pseudopokornina* with long, curved lateral spines, for which he suggested tricorninid affinities. Blumenstengel (1963) illustrated poorly-preserved but recognisable tricorninids from the Silurian of Germany. Elongate, spinose bairdioideans of the Beecherellidae (e.g. *Acanthoscapha*), an important component of the Devonian Thuringian Ecotype, were already present in the Silurian (Blumenstengel 1967).

Bandel & Becker (1975) also recognised a third, hemipelagic facies ("Entomozoan Ecotype") characterised by "fingerprint" ostracods of the Entomozooidea (Myodocopida) that are considered to have been planktonic. Becker, however, always considered the comparison with the Tertiary – Recent psychrospheric fauna to be unsuccessful or inappropriate and maintained that the Thuringian Ecotype was characteristic simply of low-energy conditions, not necessarily deep, cold or poorly oxygenated, and could be found in shallow-water as well as deep-water settings (Becker & Bless 1990; Becker *et al*. 1993; Becker 2000b).

Casier (2008) illustrated the depth distribution of the different Late Palaeozoic "ecotypes" which he renamed as "mega-assemblages" (Fig. 1), arguing that the term "ecotype" could be used for only one species. The terms Eifelian Mega-assemblage, Thuringian Mega-assemblage and Myodocopid Mega-assemblage are preferred and adopted herein. We note that Casier's (2008; 2017) illustration of "Anoxia" beneath the OMZ (Oxygen Minimum Zone) (Fig. 1) is a contradiction in terms, so that his OMZ may be intended to represent a gradient from well-oxygenated water to anoxic water.

Insert Figure 1 around here

Insert Figure 2 around here

The Thuringian Mega-assemblage (TMA) of the early Devonian existed until the Eifelian stage but was absent or weakly represented during the Givetian and early Frasnian; subsequently, beginning in the early Famennian, it acquired many new taxa and the resulting TMA persisted into the Carboniferous (Tournaisian – Dinantian) in the Palaeotethys (Lethiers & Raymond 1991). Figure 2 illustrated some examples of characteristic Late Devonian TMA species. The TMA seems to have been relatively unaffected by the Frasnian–Famennian boundary crisis (Kellwasser Event) which wiped out at least 75% of ostracod species, the extinctions mostly affecting neritic (Eifelian Mega-assemblage) taxa in deeper water as well as shallow-water settings (Casier & Lethiers 2002).

The recent study of Late Devonian ostracod palaeobiogeography by Song & Gong (2017) focused on neritic faunas and paid relatively little attention to the widely-distributed TMA, its characteristic taxa and its possible relationship with deep ocean circulation. We have plotted examples of the Devonian to Early Carboniferous TMA on palaeogeographical maps showing reconstructed tectonic plate positions. Early to Mid Devonian examples (Fig. 3) are known from Germany (Emsian: Bandel & Becker 1975; Groos-Uffenorde & Jahnke 1973), USA (New York) (Emsian: Berdan, 1990), Morocco (Emsian–Givetian: Becker *et al*. 2004), Spain (Emsian: Becker & Sánchez de Posada 1977; Becker 2000a), southern France (Feist & Groos-Uffenorde 1979), Turkey (Pontides) (Emsian: Dojen *et al*. 2004; Olempska *et al*. 2015) and Japan (Emsian: Kuwano 1987). We have also plotted on Fig. 3 the USA (Ohio) Silica Formation ostracod assemblage (Givetian: Kesling & Chilman 1978) because although not a TMA it contains taxa with possible TMA affinities (discussed further below). Late Devonian to Early Carboniferous examples (Fig. 4) are known from Germany (Famennian: Becker & Blumenstengel 1995b; Devonian-Carboniferous boundary: Becker & Blumenstengel 1995b, Becker 1999; Early Carboniferous: Gründel 1961, 1962, 1971, Becker 1990), Poland (Devonian-Carboniferous boundary: Olempska 1997); southern France (Devonian-Carboniferous boundary: Lethiers & Feist 1991); French Pyrenees (Early Carboniferous: Crasquin-Soleau *et al.* 1989; Perret *et al.* 1994); Turkey (Famennian: Nazik *et al*. 2012), Morocco/Algeria (Devonian-Carboniferous boundary: Becker 1987), Spain (Frasnian–Famennian: Sánchez de Posada *et al*. 2008), the Urals (Frasnian–Famennian: Rozhdesvenskaja 1972), China (Early Carboniferous: Ji & Chen 1987; Wang 1988), NE Russia (Omolon region, Late Famennian to Early Carboniferous: Shilo *et al*. 1984; Kolyma region: Schornikov 1993) and Tibet (Early Carboniferous: Shi 1982). Devonian TMAs are nearly all found in settings that bordered the Rheic and Palaeotethys oceans (Figs 3 and 4), as might be expected if they represent a deep-ocean fauna. Exceptions are the diverse Middle Devonian Silica Formation fauna of Ohio (4 on Fig. 3) which is composed predominantly of shallow-water taxa but includes some deep-water genera (e.g., *Acratia, Rectobairdia, Monoceratina, Aechmina*) suggesting Thuringian affinities, and NE Russian occurrences (9 on Fig. 4) of the Late Devonian to Early Carboniferous, on the edge of the Panthalassic Ocean and at a high enough palaeolatitude to reflect a possible poleward shallowing of a palaeopsychrosphere.

Insert Figure 3 around here

Insert Figure 4 around here

Palaeoecological interpretation of Thuringian Mega-assemblage taxa

Thuringian Mega-assemblage taxa are best regarded as benthonic, although some may have been nektobenthonic. Becker & Bless (1990) suggested that the kirkbyoidean taxa were probably nektobenthonic and Tricorninidae may have been occasional swimmers, but the rest were crawlers or burrowers. Somewhat confusingly, Becker & Blumenstengel's (1995a: figs 7 and 9) illustrations of many taxa of the Devonian-Carboniferous TMA are captioned as members of a pelagic fauna, although in their text they make it clear that these

were considered to be benthonic or nektobenthonic; a careful reading shows that they meant that these taxa occur in fine grained sediments accumulated below wave-base, corresponding to (hemi)pelagic depositional conditions, and not that the ostracods themselves had a pelagic mode of life.

The TMA is considered to have lived in deep water because of its co-occurrence with pelagic fauna (e.g. entomozooideans, goniatites, conodonts) in low-energy sedimentary settings, as well as morphological similarities with Tertiary–Recent psychrospheric taxa (thin shells, long spines). Absence of eye-tubercles (to indicate blindness) is sometimes taken as an indicator of deep water below the photic zone but this is very unreliable (Horne 2010). There are no morphological features in these ostracods that can indicate warm or cold water. Schornikov & Michailova (1990) discussed the functional morphology of ostracod shells with particular attention to the palaeoecology of Devonian Bythocytheridae (well-represented in the TMA, including genera such as *Berounella, Bythoceratina, Monoceratina, Nemoceratina, Paraberounella* and *Triceratina*) as well as the Tricorninidae which are closely related and possibly ancestral to the cytheroidean Family Bythocytheridae (Schornikov 1988). They argued that these taxa had partly infaunal lifestyles in very loose, fine grained sediments on the sea floor, and the elongate carapace shapes, long spines and other features represent adaptations to facilitate stability and efficient movement through such material. As pointed out by Becker (2000b) such conditions do not necessarily mean deep water; nevertheless his text-fig. 3 suggests a depth range of 1000–5000m for the Thuringian Ecotype. Becker & Bless (1990) suggested that members of the Tricorninidae may have been occasional swimmers because they have convex ventral margins and their long spines would likely have made it difficult to crawl on the sediment surface; they argued, therefore that these were not cytheroideans (since no living cytheroideans can swim), but could be placed in the palaeocopid Superfamily Drepanelloidea. This argument seems quite weak, since on the one hand it cannot be confirmed that tricorninids could swim, and on the other it cannot be ruled out that the ability to swim was possessed by at least some Palaeozoic cytheroideans but was subsequently lost in that lineage. Groos-Uffenorde (2004) described a well-preserved entomozooidean assemblage from the Late Famennian of Germany in which the specimens were pyritised, in contrast to the calcareous preservation of the associated podocopids, platycopids and palaeocopids. She concluded that the different styles of preservation in the same deposits reflected different modes of life, the entomozooideans being pelagic while the calcareous taxa (which included a few TMA taxa such as *Acratia*, *Heterma* and *Marginohealdia*) were benthonic or nektobenthonic, the unusual association arising from accumulation in a relatively shallow but protected offshore area well below storm wave-base.

Deep ocean water masses are often undersaturated with respect to Calcium Carbonate, compared to surface waters which tend to be supersaturated. The elaborate carapace ornamentation (e.g. reticulation, spinosity) typical of many Tertiary-Recent psychrospheric ostracods may facilitate the entrapment of fine calcareous particulates (e.g. coccoliths) around the ostracod shell, forming a buffer zone against dissolution by corrosive ambient waters because the calcareous debris will dissolve more readily than the calcite shell of the ostracod (Swanson 1995). While many TMA taxa typically seem to have rather smooth valve surfaces between few, large spines, so that such a function seems unlikely, well-preserved specimens often exhibit densely and finely ornamented surfaces strongly reminiscent of Tertiary–Recent psychrospheric forms. A good example is the Upper Devonian tricorninid *Tricornina (Bohemina) paragracilis* illustrated by Becker (1988) which has a densely spinose surface as well as large lateral spines. We consider it possible that fine surface ornament in TMA taxa may indeed have served to trap calcareous particles as a buffer against corrosion, while large spines, especially those directed dorsally or posteriorly, might have served to protect benthonic ostracods against predators. Benson (1988: 5) suggested that carapace spines in deep-sea ostracods are an adaptive defence “against being swallowed”. We can only speculate about the identity of organisms in the Palaeozoic deep ocean that might have

preyed particularly on ostracods (perhaps nekto-benthonic conodont animals, ammonoids or fishes), thus providing the selection pressure that would lead to increased spinosity.

The assumption that deep waters must have been oxygen-deficient (e.g. Lethiers & Crasquin 1987; Lethiers & Feist 1991; Becker 2000b) is problematic in view of the relatively high taxonomic diversity of the TMA and we consider it far more likely that such faunas represent well-oxygenated bottom waters. Lethiers & Crasquin (1987) considered the TMA in the Famennian–Tournaisian to represent deep, calm, cold waters, deficient in dissolved oxygen but rich in dissolved silica ; however, they acknowledged that this was inconsistent with the Tertiary–Recent psychrospheric fauna's environment in the Atlantic Ocean where the cold bottom waters are well-oxygenated. With regard to the functional morphology of the prominent spines that are characteristic of many TMA taxa, they rejected suggestions that they aided a planktonic (Bandel & Becker 1975), nektonic (Bless & Michel 1967) or nekto-benthonic (Gooday & Becker 1979) mode of life, arguing that the majority of species must have been benthonic crawlers; they speculated that hollow spines might have served to augment the internal surfaces for oxygen exchange and thus facilitate life in oxygen-poor environments. The argument for silica-rich waters rests largely on comparison with the living freshwater cytheroidean *Kavalacythereis* which bears long, hollow spines similar to those of TMA genera such as *Rectonaria* and inhabits calm waters rich in organic silica in Lake Tanganyika (Lethiers & Crasquin 1987). Although there are no morphological features that indicate dissolved oxygen levels, the "platycopid signal " interpretation of Lethiers & Whatley (1994, 1995) is worth considering, in spite of criticism and alternative explanations with respect to Mesozoic to Recent applications of their method (Brandão & Horne 2009; Horne *et al*. 2011). Based on the observation that filter-feeding ostracods are better-equipped than others to survive in oxygen-deficient waters because they are more efficient at circulating water across their respiratory surfaces, Lethiers & Whatley (1994, 1995) considered Devonian assemblages to show low oxygen in the Frasnian, increasing across the Frasnian-Famennian boundary, and well-oxygenated waters at the Devonian-Carboniferous boundary. They regarded as filter-feeders not only the Platycopida (Platycopina and Metacopina) but also the Palaeocopida and the Kloedenelloidea (which they considered to have morphological characteristics in common with both palaeocopids and platycopines; we regard them as platycopids) and the Paraparchitoidea (which are similarly discussed as being of uncertain affinity; we regard them as palaeocopes). Lethiers & Whatley (1994) stated that c. 70% of neritic ostracod species disappeared during the Frasnian–Famennian crisis, with deposit feeders becoming very rare and the percentage of filter-feeders reaching as high as 88%; pelagic entomozooideans survived it, probably because they lived in the upper, oxygenated part of the water column. They considered low oxygen levels, linked with warm climate, to be the limiting factor for ostracod assemblages throughout the Frasnian. They also commented on the TMA, stating that application of their method showed these faunas to have >40% filter-feeders, which they regarded as indicating oxygen levels of c. 3 ml/l. This is strange, because their Fig. 2 shows that >60% filter-feeders corresponds to 3ml/l while between 40% and 50% filter-feeders would suggest >4 ml/l dissolved oxygen, i.e. quite well oxygenated; however, although they state that their method was applied "in the strictest manner" they appealed to "special circumstances" (Lethiers & Whatley 1994: 66) concerning the specialised adaptations of deposit-feeding podocopids to the low oxygen levels at bathyal depths, and this seems to explain their lower estimate of dissolved oxygen. Even accepting their estimate of c. 3 ml/l it must be pointed out that, while this could represent an Oxygen Minimum Zone such as is found in the western North Atlantic today, such waters are far from anoxic and are capable of sustaining diverse deposit-feeding podocopids as well as filter-feeding platycopids (Brandão & Horne 2009). Olempska (2008) has shown that palaeocopids were almost certainly not filter-feeders, because they have mandibular scars indicating podocopid-style mandibulae. Moreover, Tibert & Dewey (2006) described a healdioid genus (*Velatomorpha*) which clearly has a frontal and a mandibular scar anterior to the adductor muscle scars (they label them both as frontal scars); if this is really a metacopine healdioid it casts doubt on whether all Metacopina were filter feeders.

Nevertheless there are “platycopid signals” associated with the Devonian crises. Casier & Lethiers (1998), in their study of the Devil’s Gate Pass section (Nevada, USA) particularly noted an abundance of Kloedenelloidea (Platycopina) in the earliest Famennian assemblage – one of these, *Knoxiella*? *rauseri* is marked as a “lazarus” species which persisted through the Frasnian-Famennian crisis and others (species of *Knoxiella*, *Indivisia* and *Marginia*) are among the earliest new appearances in the Famennian. This may be a true “platycopid signal” analogous to that seen across the mid-Cretaceous Cenomanian-Turonian Boundary Event (Oceanic Anoxic Event 2) (Horne *et al*. 2011). In Poland, Olempska (1997) documented changes in ostracods across the Devonian-Carboniferous boundary (through the Hangenberg Event), showing a temporary disappearance of the TMA and the Myodocopid Mega-assemblage (both re-appearing in the early Tournaisian) when they are replaced by a low diversity dominance of metacopids (*Healdia*) suggested to represent a platycopid signal *sensu* Lethiers & Whatley (1994). An absence of tricorninids indicates that the TMA here is quite a shallow one. She observed that “The Hangenberg anoxic event did not result in a global extinction of the Thuringian-type ostracods but only in their local disappearance in some areas” (Olempska 1997: 308). In both of these cases consideration should also be given to Horne *et al*.’s (2011) alternative interpretation of Mesozoic platycopid signals, that they signify the movement of oligotrophic oceanic waters onto the shelf during marine transgressions. Some of these ideas are further developed below.

Late Devonian anoxic events

Several authors have proposed that the marine crises in the Late Devonian, specifically the Kellwasser events in the Frasnian-Famennian boundary interval and the Hangenberg Event in the Devonian-Carboniferous boundary interval, were the result of shallow-water anoxia due to upwelling or spread of anoxic bottom water from the ocean. Riquier *et al.* (2006) argued that in the Lower Kellwasser Event oceanic anoxia was driven by increased land-derived nutrient flux to the ocean, resulting in enhanced primary productivity, while the Upper Kellwasser Event was caused by oxygen-deficient deep ocean water spilling into shallow waters. Joachimski & Buggisch (1993) suggested that warm Frasnian climate resulted in increased production of warm saline water (sinking, denser, more saline waters formed by evaporation in tropical epicontinental seas) forming intermediate or bottom water masses. These warm waters would be less oxygenated and so the Oxygen Minimum Zone (OMZ) would expand and intensify, leading to enhanced burial of organic carbon where it impinged on the sea floor. The evidence of the ostracods is more consistent with the idea of Warm Saline Intermediate Water (rather than Warm Saline Deep Water), perhaps more or less coincident with the OMZ, underlain by denser Cold Deep Water formed by cooling at high latitudes. Bond & Wignall (2008) concluded that a major sea-level rise in the late Frasnian coincided with spreading anoxic facies and major extinctions (the Upper Kellwasser Event), continuing across the Frasnian-Famennian boundary, and was terminated by sea-level fall in the early Famennian; deep-water conodonts suffered major losses in this event.

Chen *et al*. (2013) proposed (1) in the latest Frasnian, sudden oceanic overturn (oxygenated surface waters driven down into the basins, anoxic bottom waters driven upwards to the surface) at the onset of sea-level fall (see Fig.5A), then (2) in the earliest Famennian, long-lasting photic zone euxinia consequent on high productivity and organic carbon burial during major sea-level rise and finally (3) rapid oxygenation of bottom waters as climate cooled and sea-levels fell with the onset of extensive Gondwana glaciation.

Insert Figure 5 about here.

Shallow-water eutrophication consequent on increased nutrient loading in the ocean has been invoked as the cause of anoxia in the water column during both the Kellwasser events (Carmichael *et al*. 2014) and the succeeding Hangenberg Event (Late Famennian) just before the Devonian-Carboniferous boundary (Carmichael *et al*. 2016), challenging previous

suggestions of upwelling of anoxic bottom waters (e.g. Caplan & Bustin 1999). Carmichael *et al.*'s (2016: fig. 14) model shows surface water hypoxia in both coastal and open ocean settings, overlying well-ventilated deeper ocean water (see Fig. 5B). This is consistent with evidence of significant extinctions of neritic ostracods while the deep TMA remained relatively unaffected (Becker & Blumenstengel 1995a). House's (2002) otherwise comprehensive discussion of the causes and consequences of Devonian extinction events seems to have ignored the extensive and well-documented ostracod evidence, so that his discussion of dysoxic or anoxic conditions in the water column overlooks the persistence of the TMA through these events.

In the late Frasnian there were three major ostracod assemblages: (1) Eifelian Mega-asemblage benthonic ostracods occupying the shelf sea-floors, (2) TMA benthonic ostracods living in bathyal depths on the outer shelf and continental slopes and (3) the pelagic Myodocopid Mega-assemblage of entomozooideans and other myodocopes such as cypridinoideans (Casier, 2008; 2017) and bolbozoids (Groos-Uffenorde et al., 2000) living in the water column of the open ocean and shelf margins. At the Schmidt Quarry in Germany the Kellwasser Event wiped out the pelagic myodocopid (entomozooidean) fauna but the shallow benthonic podocopids of the Eifelian Mega-assemblage survived (Casier & Lethiers 1998; Casier *et al*. 1999). This suggests anoxia in the mid water column in the open ocean, perhaps encroaching on the outer shelf, but not affecting all shallow shelf areas; if this occurred during high sea-level then the spreading OMZ could even have been overlying oxygenated shelf bottom waters. Casier (2004) argued that although 75% of marine ostracod taxa went extinct at the Frasnian-Famennian boundary, the survival of several benthonic species shows that very shallow and surface waters were not so affected. The above-mentioned persistence of the TMA also argues for well-ventilated deep waters. To take account of the ostracod evidence we propose a new model for Late Devonian anoxic events (Fig. 5C, Fig. 6) which shows a mid water column OMZ and oxygenated Cold Deep Water, and which leads us to further discussion of the nature of oceanic circulation in the Devonian.

Insert Figure 6 around here

Deep ocean circulation in the Devonian

Copper (1986) argued that the closure of a "Frasnian ocean" (with low-latitude circum-equatorial flow of warm water) between Euramerica and Gondwana resulted in currents along the western margins of the continents bringing cold water from high to low latitudes, as well as the development of restricted circulation and euxinic conditions in warm-water basins on the eastern margins. He also suggested that glaciation in the Famennian, with consequent sea-level fall, might have introduced cold waters to tropical shelf areas. The "Frasnian ocean" equates to the Rheic ocean, but its closure cannot explain deep cold water in the Palaeotethys in the Famennian because more recent plate tectonics reconstructions of Devonian palaeogeography (e.g., Golonka 2002; Golonka & Gaweda 2012; Domeier & Torsvig 2014) show a more open Rheic Ocean contiguous with the Palaeotethys Ocean, with the closure of Copper's "Frasnian Ocean" not taking place until the Carboniferous.

The ostracod evidence does not seem consistent with a poorly ventilated thermospheric ocean with oxygen-deficient bottom water. It does seem consistent with a stratified ocean with cool, well-oxygenated deep waters formed by sinking in high latitudes, overlain by warm surface waters and an OMZ which does not extend to the deep ocean floor. Lethiers & Raymond (1991) considered it necessary to invoke the presence of a Gondwana ice cap to generate cold deep water currents flowing through the Palaeotethys ocean. In fact polar ice caps or the formation of high-latitude sea-ice are not essential for the generation of cold deep water masses, which depend on density differences (controlled by temperature and salinity) with surrounding waters and can form in sea-surface temperatures of <10^{o}C at 34.5 salinity, or <5^{o}C at 33.5 salinity (Wilde & Berry 1984). Modern North Atlantic Deep Water, which

does not require sea-ice for its formation, has a temperature of 2.0-3.5 ^{o}C and a salinity of 34.9 – 35.00, while Antarctic Bottom Water, the formation of which does involve salinity increase through sea-ice formation, has a temperature of -1.0 ^{o}C and a salinity of >34.61 (Gordon 2001; Toggweiler & Key 2003). Nevertheless it is worth noting that glaciation was probably an effective influence on sea-level fluctuations around the Frasnian-Famennian boundary (Isaacson *et al*. 2008) as well as later in the Famennian, throughout the Carboniferous and into the early Permian. Modelling of Late Devonian climate by de Vleeschouwer *et al*. (2014) indicates mean winter (DJF) SSTs <10^{o}C at latitudes higher than 70^{o}N in the northern hemisphere and 75^{o}S in the southern hemisphere; they suggest seasonal sea-ice extending to 70^{o}N and 80^{o}S. This provides a plausible setting for high-latitude downwelling centres where cold deep water was formed (Figs 7, 8).

Devonian deep ocean circulation in the southern hemisphere might have been somewhat analogous to the present-day Antarctic Circumpolar Current (also known as the West Wind Drift) which is driven by westerly winds and that extends from the surface to depths of 2–4 km between latitudes 40 and 60^{o}S (Rintoul 2009). Such a current in the Devonian could have entered the western end of the Rheic Ocean at around latitude 40^{o}S and would then have been forced northwards by the northern continental margins of Gondwana, through the Palaeotethys and ultimately rejoining the Panthalassic ocean in equatorial latitudes (Figs 7, 8). A similar Arctic Circumpolar Current would have been unimpeded by continents above 60^{o}N and perturbed only by the Siberian plate between 40 and 60^{o}N. A southern hemisphere current flowing eastwards between 40 and 50^{o}S in the Early Devonian could have moved cool (surface) to cold (deep) water eastwards between Euramerica and Gondwana, but it would then have been forced northwards through the Palaeotethys ocean by the northern margin of Gondwana and thence into the Panthalassic Ocean in equatorial latitudes (Fig. 7). The proximity of this current to the epicontinental sea where the Middle Devonian Silica Formation assemblages of Ohio existed (location 4 on Fig. 3) is of particular interest. Such a massive and cool current, extending from the surface to the ocean floor, could have provided the opportunity for shelf taxa to gradually adapt and move into deep water without encountering significant barriers (such as a marked thermocline) to migration. Such a setting can be envisaged for the origin of the palaeopsychrospheric fauna, without necessarily suggesting that the Silica Formation itself represents either the centre or timing of that origin. The diverse Silica Formation ostracod assemblages are mainly shallow shelf in character but they do include a few taxa with TMA affinities, such as *Aechmina*, *Acratia*, *Rectobairdia*, *Acanthoscapha* and bythocytherids like *Monoceratina, Cornigella* (which could have tricorninid affinities although Kesling & Chilman (1978) placed it in the Bolliidae, Drepanelloidea) and *Sigynus*, a rare, small palaeocopid with a pair of large dorso-lateral spines.

Insert Figure 7 around here

Insert Figure 8 around here

The same current, transporting deep, cold water through the Palaeotethys Ocean to equatorial regions, could have persisted in the Late Devonian although the ocean basin was becoming increasingly constricted (Fig. 8), foreshadowing closure in the Carboniferous which must have caused a major reorganisation of ocean circulation.

An alternative to having surface currents bringing cold water from high to low latitude as envisaged by Copper (1986) is the upwelling of deep cold water at continental margins. Steady (perhaps seasonal) longshore winds, with the land on the left in the northern hemisphere and on the right in southern hemisphere, create a net offshore movement of the uppermost tens of metres of the water column (Ekman transport), and the water moving away from the coast is replaced by intermediate or deep water upwelling from below (Totman Parrish & Curtis 1982; Servais *et al*. 2014). The atmospheric circulation indicated by Vleeschouwer *et al*. (2014) for southern hemisphere summer shows the Inter-Tropical Convergence Zone running south of the equator through Euramerica and along the northern

margins of Palaeo-Tethys, with anticyclonic winds circulating anticlockwise around highs situated over the Palaeotethys; the resulting longshore winds could have produced upwelling zones on both the northern and southern margins of the W-E oriented Palaeotethys. Accordingly we have indicated potential upwelling sites on Early and Late Devonian palaeogeographical reconstructions (Figs 7 and 8), noting possible coincidence with sites where palaeopsychrospheric assemblages are known.

Conditions for preservation of palaeopsychrospheric assemblages

Taking account of the evidence reviewed above, we consider it possible that a palaeopsychrospheric TMA ostracod fauna was widespread and diverse in the deep ocean (bathyal – abyssal) in the Devonian, but since nearly all such depositional settings have been lost due to subduction, we must address the question of why such a fauna has left even a sporadic fossil record. Lethiers & Feist (1991) suggested that TMA faunas were associated with deep, cold water and oxygen minimum zones in continental margin/slope settings but that in high latitudes (with colder surface waters) or in upwelling regions they could become more abundant on the outer continental shelf. As discussed above, we consider it more likely that such faunas inhabited well-oxygenated waters, but it is not difficult to reconcile such a view with the other aspects of Lethiers & Feist's scenario. We propose that a palaeopsychrospheric fauna could spread up the continental slope and into outer shelf settings, where there is a greater likelihood of its fossil record being preserved, when (a) sea level is high and /or (b) longshore winds result in Ekman transport driving shallow waters away from the coast, creating upwelling cells of deep, cold water that cause shoaling of the thermocline. In equatorial regions today, Sea Surface Temperatures in upwelling areas can be as much as 10ºC cooler than where there is no upwelling (Brown *et al*. 1980; Zachos *et al*. 1994). In the modern ocean, where upwelling deep, cold, nutrient-rich waters stimulate high primary productivity in the surface waters, an expanded and intensified oxygen minimum zone often develops but is not necessarily exactly coincident with the upwelling cell. In the equatorial Somali Basin of the Arabian Sea today, dense Circumpolar Deep Water (below 3,000m depth) formed around Antarctica is characterised by low temperature (<1.1ºC), low salinity (<34.725) and high dissolved oxygen (>175 µM), and is overlain by Indian Ocean Deep Water (upper limit 2000m) with low temperature (between 1.4 and 1.9ºC), higher salinity (34.730 to 34.745) and lower oxygen content (150 to 170 µM) (Dengler *et al*. 2002). In contrast, surface water temperatures in the region are typically between 20 and 30ºC, salinities between 35.7 and 36.3 (Currie 1992). Note that in terms of oceanic waters, the use of "high" and "low" typically refers to very small differences in temperature and salinity which are nevertheless highly significant in determining the density differences that characterise different water masses. It is noteworthy that in the Somali Basin example given above, the deep waters have lower salinity than the surface waters; they are dense enough to be deep waters because they are so much colder than the surface waters. Between these deep water masses and the surface waters in the Arabian Sea, high-salinity waters from the marginal seas (Red Sea, Persian Gulf) form intermediate waters with which a thick oxygen minimum zone (oxygen concentration < 4.5 µM) is approximately coincident at depths between 150 and 2000m (Morrison 1997; Morrison *et al.* 1999). However, contrary to the expectation that minimum oxygen concentrations would occur immediately under waters with the highest productivity, the oxygen minimum zone is not directly coincident with the upwelling and is shifted eastwards from the highest productivity region, possibly due to the effects of surface currents (Resplandy *et al*. 2012; McCreary *et al*. 2013). If we apply a similar scenario to Devonian settings it is possible to envisage a situation in which upwelling of deep, cold, nutrient-rich, oxygenated water stimulates high productivity in surface waters close to the continental margin, while the resulting oxygen minimum zone is shifted towards the open ocean and does not impinge on the sea floor of the outer shelf and continental slope.

Dependence on upwelling cells to permit up-slope migration could explain why the Thuringian assemblage can occur, but does not always occur, in outer platform – upper slope depths and settings (Fig. 9); these are preservational windows into the deep sea benthonic fauna which is otherwise lost. This model can also help to explain the sporadic Late Palaeozoic – Early Mesozoic fossil record of the palaeopsychrosphere while allowing for its persistent existence and the continuity of the fauna, even through the crises of the Kellwasser and Hangenberg events.

Ostracods are also unlikely to be preserved if deposited in palaeo-depths below the lysocline, where waters are undersaturated with respect to Calcium Carbonate, although this does not preclude their having lived at such depths. The Carbonate Compensation Depth (below the lysocline) is typically at 3.5 to 4.5 km depth in the Pacific and Indian oceans today, deeper in parts of the Atlantic; at high latitudes it is shallower. However, as has been demonstrated, e.g. by Yasuhara et al. (2008) and by Jellinek *et al.* (2006), ostracods can live at depths > 4,000m in the modern ocean, but their shells are unlikely to be preserved due to the corrosive nature of the water below the lysocline.

Conclusions

Having reviewed the ostracod evidence in the context of interpretations of Devonian palaeogeography and paleoceanography, we find the idea that such a fauna inhabited poorly-oxygenated deep waters difficult to accept. On the contrary, we consider that the taxonomic and morphological characteristics of the Thuringian Mega-assemblage, its distribution around the margins of the Rheic and Palaeotethys oceans and its survival through Late Devonian crises that resulted in extinctions of neritic and pelagic taxa, are all consistent with the notion of a palaeopsychrospheric fauna inhabiting bathyal to abyssal, cold, well-oxygenated waters. The Thuringian Mega-assemblage may have originated in the late Ordovician or Silurian and was well-established by the early Devonian, then persisting until the Mid Triassic. Its long-term survival suggests that a palaeopsychrosphere may have provided refugia for ostracods and other organisms during the Late Devonian and end-Permian mass extinction events, as suggested by Benson (1988). This raises the question of why the Thuringian Mega-assemblage became extinct in the Late Triassic and was not replaced by the modern psychrospheric ostracod fauna until the Early Cenozoic; we hope to address this in future work but for now we suggest that a possible explanation may lie in the decline or absence of deep, cold oceanic circulation during the Mesozoic greenhouse period.

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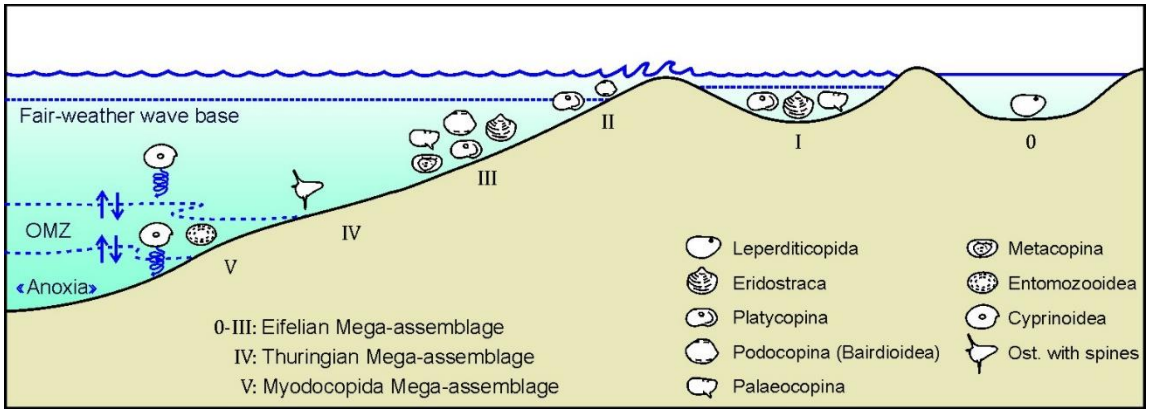

Fig. 1: Location of the different ostracod mega-assemblages along the platform (redrawn, with minor modifications, from Casier 2008).

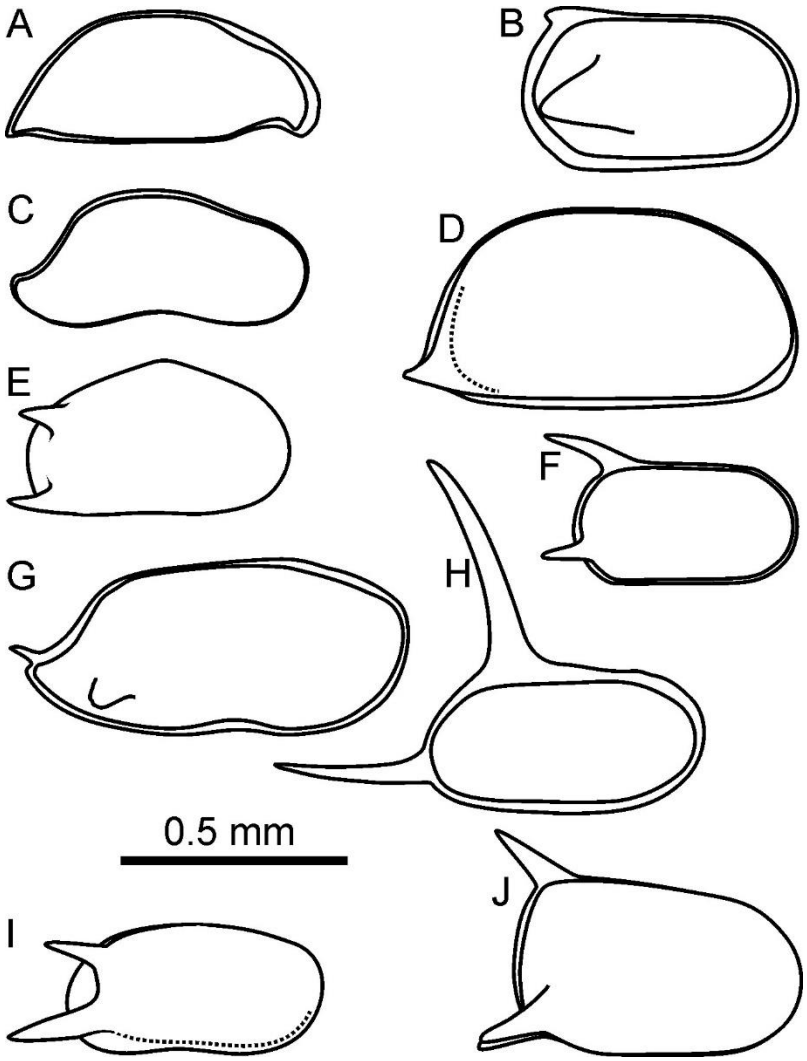

Fig. 2. Illustrations of some representative Thuringian Mega-assemblage taxa from the Devonian-Carboniferous transition of Montagne Noire, France (drawn from illustrations in Lethiers & Feist 1991); all carapaces, right side lateral view. A: *Acratia (Cooperuna) cooperi*; B: *Aurigerites blumenstengeli nigermontanus*; C: *Bairdiolites festivus*; D: *Gerodia ratina*; E: *Healdiopsis thuringensis thuringensis*; F: *Orthonaria neotridentifer*; G: *Rectobairdia venterba*; H: *Rectonaria muelleri*; I: *Timorhealdia nitidula nitidula*; J: *Triplacera triquetra*.

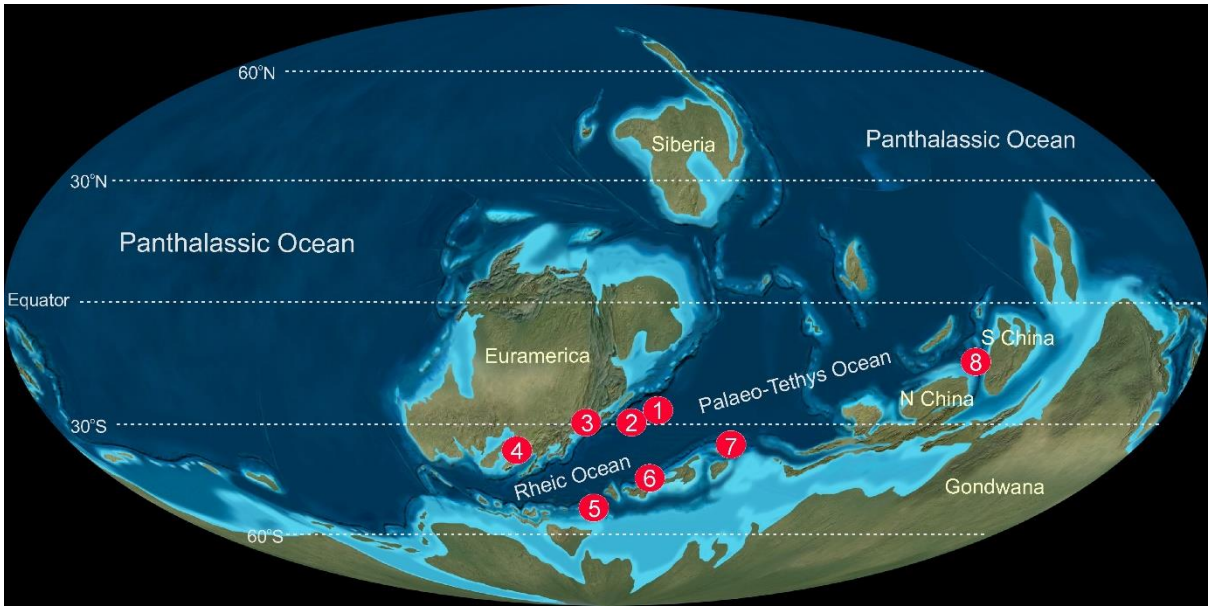

Fig. 3. Locations of Thuringian Mega-assemblages in the Early to Mid Devonian; Early Devonian palaeogeography (Colorado Plateau Geosystems, Inc.). 1: Germany; 2: France; 3: New York; 4: Ohio; 5: Morocco; 6: Spain; 7: Turkey; 8: Japan. European terranes are variously considered to have been within the Rheic Ocean or on its borders with either the Euramerican or Gondwana continents (e.g. Maillet et al., 2013; Sachanski et al., 2015). According to Domeier & Torsvik (2014) the Palaeozoic affinities of Japan are uncertain and it could be placed adjacent to either the North China or South China plates.

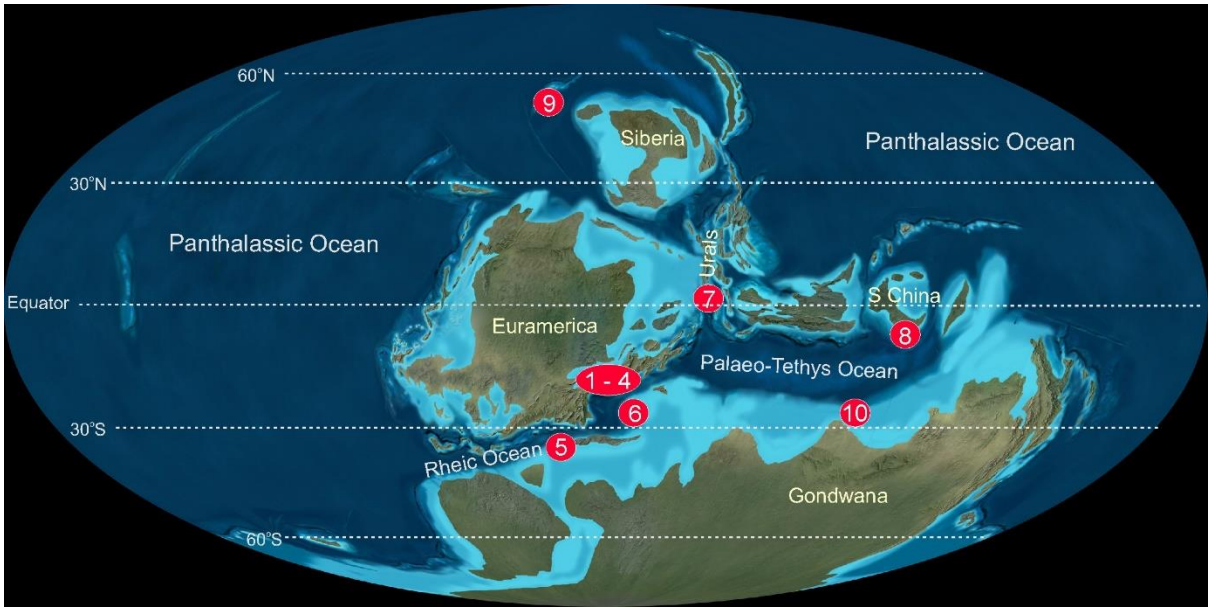

Fig. 4. Locations of Thuringian Mega-assemblages in the Late Devonian to Early Carboniferous; Late Devonian palaeogeography (Colorado Plateau Geosystems, Inc.). 1: Germany; 2: Poland; 3: S France; 4: Turkey; 5: Morocco-Algeria; 6: Spain; 7: Urals; 8: S China; 9: NE Russia; 10: Tibet.

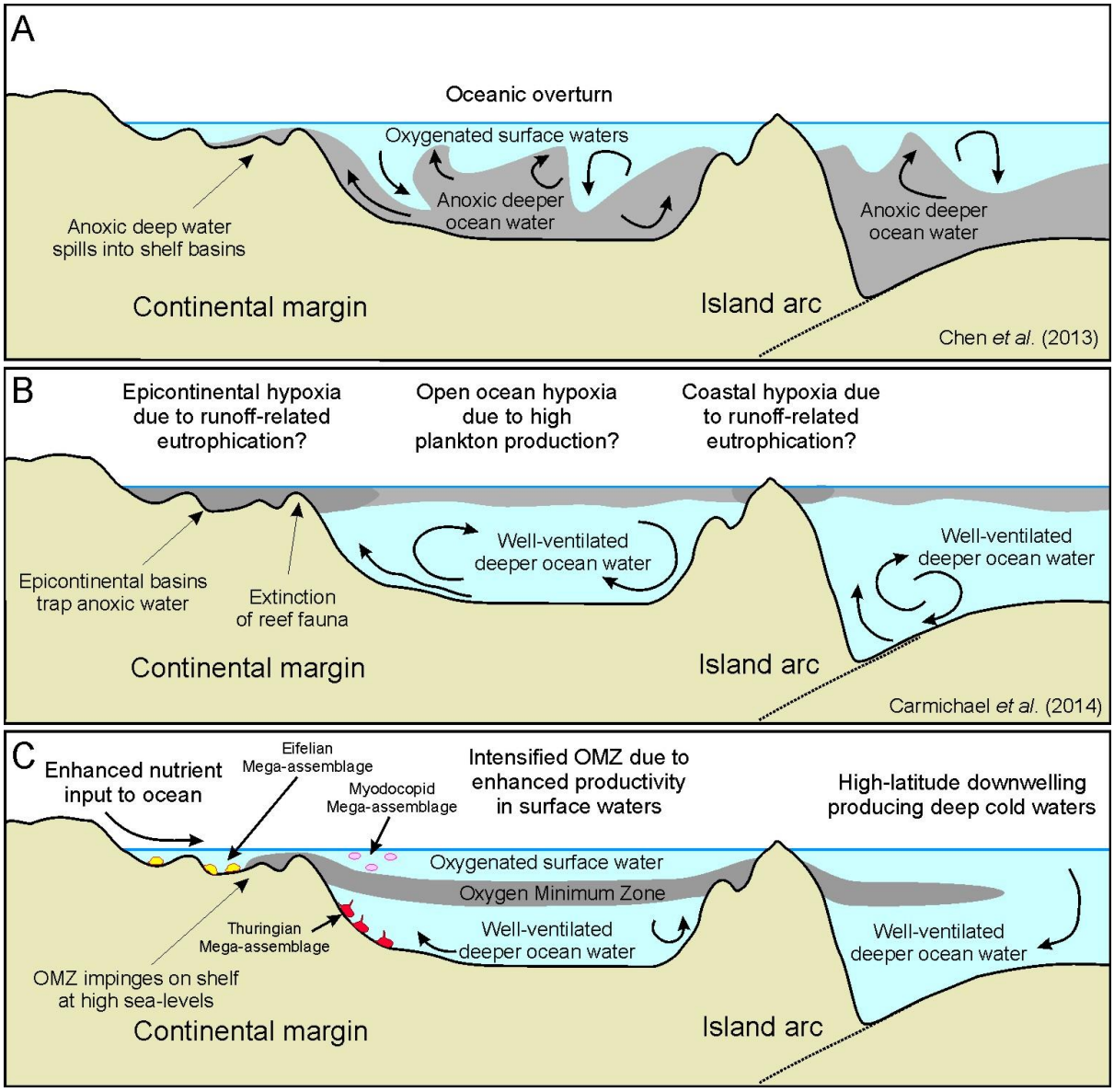

Fig. 5. Three alternative models for the Frasnian–Famennian crisis. A: sudden oceanic turnover bringing deep anoxic water onto the shelves (after Chen *et al*. 2013); B: well-oxygenated deep water, with eutrophication resulting in hypoxia / anoxia in surface and shelf waters (after Carmichael *et al*. 2014); C: a mid water column oxygen minimum zone between oxygenated surface and deep waters, expanding onto the shelves in response to enhanced productivity (see Fig. 6 for development of this model).

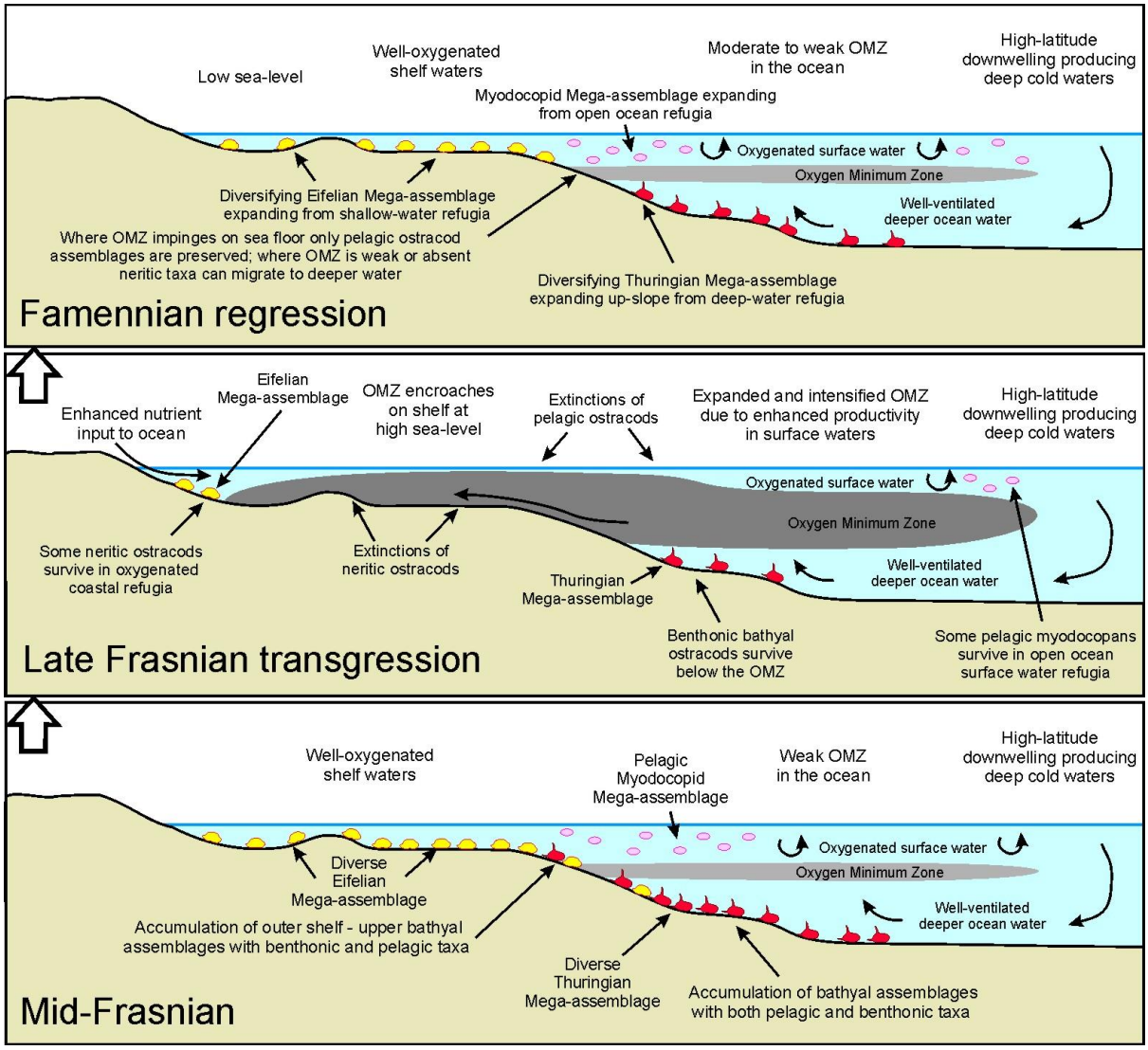

Fig. 6. A new model for the Frasnian–Famennian crisis.

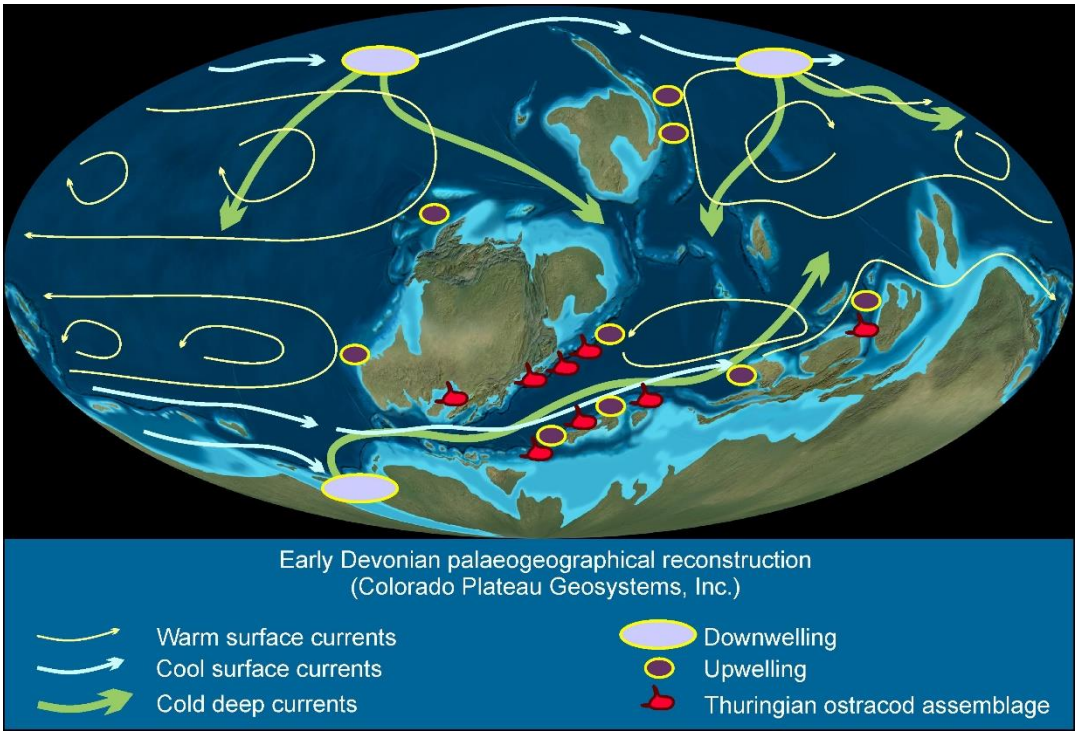

Fig. 7. Early Devonian palaeogeography (Colorado Plateau Geosystems, Inc.) showing distribution of deep water (Thuringian) ostracod faunas in the Early to Mid Devonian, with speculative addition of main components of ocean circulation (downwelling and upwelling sites based on modelling by de Vleeschouwer *et al*. 2014).

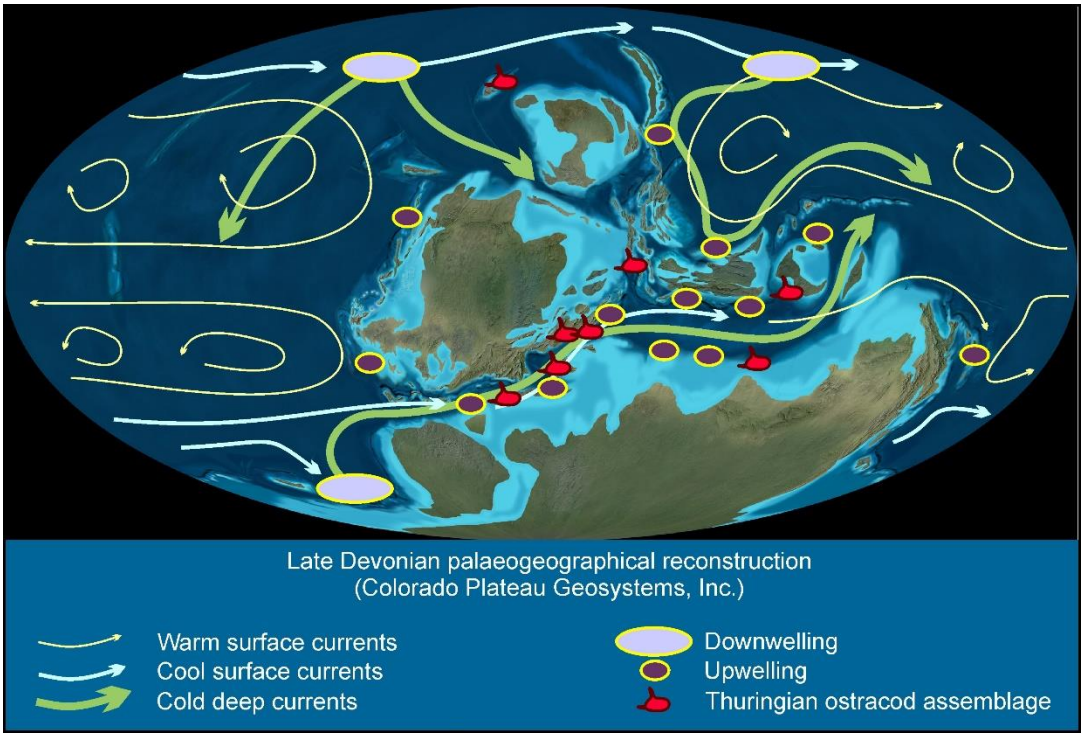

Fig. 8. Late Devonian palaeogeography (Colorado Plateau Geosystems, Inc.) showing distribution of deep water (Thuringian) ostracod faunas in the Late Devonian and earliest Carboniferous, with speculative addition of main components of ocean circulation (downwelling and upwelling sites based on modelling by de Vleeschouwer *et al*. 2014).

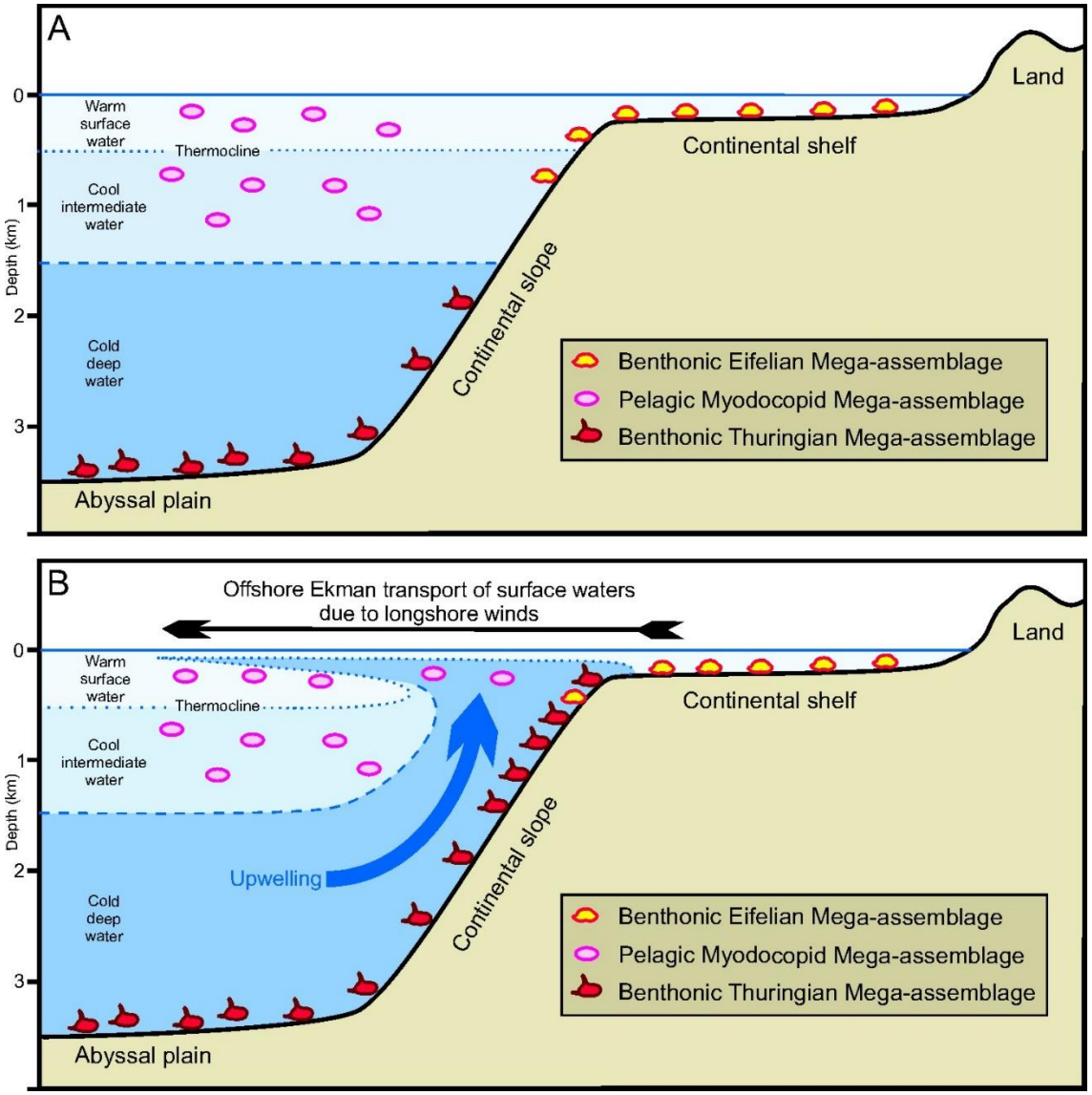

Fig. 9. Schematic diagrams to illustrate a possible palaeoceanographical setting for the preservation of Palaeozoic palaeopsychrospheric assemblages. A: Stratified ocean with warm surface water underlain by cool intermediate and cold deep water masses formed by mid- to high-latitude downwelling of surface waters; the palaeopsychrospheric fauna (TMA) is widespread on the abyssal plain and continental slope but assemblages have little chance of being preserved due to post-mortem dissolution below the lysocline and, ultimately, subduction of ocean floor. B: In certain areas, steady longshore winds cause movement of surface waters away from the coast and create upwelling cells of deep water, allowing the TMA to spread up the continental slope and even onto the outer shelf, greatly increasing its likelihood of preservation.

Table 1. Characteristic taxa of the Thuringian Mega-assemblage in the Devonian and Early Carboniferous; adapted from Lethiers & Crasquin (1987), Lethiers & Raymond (1991) and Lethiers & Feist (1991); higher classification is revised and to some extent follows Horne (2005). Genera with * have species in the Eifelian Mega-assemblage as well as in the Thuringian Mega-assemblage.

Order	Suborder	Superfamily	Family	Genera
Podocopida	Cytherocopina	Cytheroidea	Tricorninidae	*Bohemina* *Ovornina* *Spinella* *Tricornina*
			Bythocytheridae	*Berounella* *Bythoceratina* *Monoceratina* *Nemoceratina* *Paraberounella* *Triceratina*
			Quasillitidae	*Absina* *Heterma*
	Bairdiocopina	Bairdioidea	Bairdiidae	*Acratia** *Bairdia** *Bairdiolites** *Bohlenatia* *Ceratacratia* *Clinacratia* *Costabairdia** *Processobairdia*
			Beecherellidae	*Acanthoscapha* *Beecherella*
	Sigilliocopina	Bairdiocypridoidea	Bairdiocyprididae	*Healdianella** *Praepilatina**
			Gerodiidae	*Baschkirina** *Gerodia* *Paragerodia*
			Rectonariidae	*Cristanaria* *Necrateria* *Orthonaria* *Rectonaria* *Rectoplacera* *Triplacera*
			Pachydomellidae	*Ampuloides* *Karinadomella* *Pachydomella*
		Sigillioidea	Sigilliidae	*Grammia* *Microcheilinella**
Platycopida	Metacopina	Healdioidea	Healdiidae	*Aurigerites* *Healdia** *Healdiopsis,* *Timorhealdia* *Marginohealdia*
Palaeocopida	Kirkbyocopina	Kirkbyoidea	Arcyzonidae	*Villozona*
			Amphissitidae	*Amphissites** *Kullmanissites* *Neochilina* *Sinessites*
	Binodocopina	Drepanelloidea	Drepanellidae	*Limbatula*
	Beyrichicopina	Hollinelloidea	Hollinellidae	*Hollinella** *Parabolbina*
		Aparchitoidea	Aparchitidae	*Fellerites*
			Graviidae	*Selebratina*